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Abstract: Dispersal is a key process governing the dynamics of socially and spatially structured populations and involves three distinct stages: emigration, transience and settlement. At each stage, individuals have to make movement decisions, which are influenced by social, environmental and individual factors. Yet, a comprehensive understanding of the drivers that influence such decisions is still lacking, particularly for the transient stage during which free-living individuals are inherently difficult to follow. Social circumstances such as the likelihood of encountering conspecifics can be expected to strongly affects decision-making during dispersal, particularly in territorial species where encounters with resident conspecifics are antagonistic. Here, we analysed the movement trajectories of 47 dispersing coalitions of Kalahari meerkats Suricata suricatta through a landscape occupied by constantly monitored resident groups, while simultaneously taking into account environmental and individual characteristics. We used GPS locations collected on resident groups to create a georeferenced social landscape representing the likelihood of encountering resident groups. We used a step-selection function to infer the effect of social, environmental and individual covariates on habitat selection during dispersal. Finally, we created a temporal mismatch between the social landscape and the dispersal event of interest to identify the temporal scale at which dispersers perceive the social landscape. Including information about the social landscape considerably improved our representation of the dispersal trajectory compared to analyses that only accounted for environmental variables. The latter were only marginally selected or avoided by dispersers. Before leaving their natal territory, dispersers selected areas frequently used by their natal group. In contrast, after leaving their natal territory, they selectively used areas where they were less likely to encounter unrelated groups. This pattern was particularly marked in larger dispersing coalitions and when unrelated males were part of the dispersing coalition. Our results suggest that, in socially and spatially structured species, dispersers gather and process social information during dispersal, and that reducing risk of aggression from unrelated resident groups outweighs benefits derived from conspecific attraction. Finally, our work underlines the intimate link between the social structure of a population and dispersal, which affect each other reciprocally.

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# Socially informed dispersal in a territorial cooperative breeder

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**ABSTRACT**

1. Dispersal is a key process governing the dynamics of socially and spatially structured populations, and involves three distinct stages: emigration, transience, and settlement. At each stage, individuals have to make movement decisions, which are influenced by social, environmental, and individual factors. Yet, a comprehensive understanding of the drivers that influence such decisions is still lacking, particularly for the transient stage during which free-living individuals are inherently difficult to follow.

2. Social circumstances such as the likelihood of encountering conspecifics can be expected to strongly affects decision making during dispersal, particularly in territorial species where encounters with resident conspecifics are antagonistic. Here we analyzed the movement trajectories of 47 dispersing coalitions of Kalahari meerkats (*Suricata suricatta*) through a landscape occupied by constantly monitored resident groups, while simultaneously taking into account environmental and individual characteristics.

3. We used GPS locations collected on resident groups to create a geo-referenced social landscape representing the likelihood of encountering resident groups. We used a step-selection function to infer the effect of social, environmental and individual covariates on habitat selection during dispersal. Lastly, we created a temporal mismatch between the social landscape and the dispersal event of interest to identify the temporal scale at which dispersers perceive the social landscape.

4. Including information about the social landscape considerably improved our representation of the dispersal trajectory, compared to analyses that only accounted for environmental variables. The latter were only marginally selected or avoided by dispersers. Before leaving their natal territory, dispersers selected areas frequently used by their natal group. In contrast, after leaving their natal territory, they selectively used areas where they

were less likely to encounter unrelated groups. This pattern was particularly marked in larger dispersing coalitions and when unrelated males were part of the dispersing coalition.

5. Our results suggest that, in socially and spatially structured species, dispersers gather and process social information during dispersal, and that reducing risk of aggression from unrelated resident groups outweighs benefits derived from conspecific attraction. Finally, our work underlines the intimate link between the social structure of a population and dispersal, which affect each other reciprocally.

**Keywords:** Conspecific avoidance, informed dispersal, movement, social landscape, step selection, *Suricata suricatta*

## INTRODUCTION

Dispersal of individuals is an important process governing the dynamics of spatially and socially structured populations (Hanski 1999; Clobert *et al.* 2001). Through emigration and immigration, dispersal can also affect local allele frequencies, alter the structure of existing social groups, and lead to the formation of new groups (Clobert *et al.* 2001; Bateman *et al.* 2012). Improving our understanding of dispersal is therefore critical as we strive for better forecasting of long-term population trends and viability (Bowler & Benton 2005; Ronce 2007).

The dispersal process can be divided into three phases: emigration from the natal territory; transience; and settlement in a new territory (Bowler & Benton 2005). Each phase is dependent on different individual, environmental, and social drivers, and our ability to understand the mechanisms of dispersal relies on our ability to account for and understand the factors affecting the movement of individuals in each of the three phases (Wiens 2001; Schick *et al.* 2008; Clobert *et al.* 2009). Due to the difficulty of following individuals under natural conditions, past studies have mainly focused on the causes and consequences of emigration from the natal territory (Stephens *et al.* 2005; Cote & Clobert 2007, 2010). For instance, rates of emigration have been shown to be density-dependent, to relax local competition, and to favour inbreeding avoidance (Holekamp & Sherman 1989; Perrin & Mazalov 2000; Bowler & Benton 2005; Bateman *et al.* 2012) . In contrast, we have much less information about the mechanisms and strategies that individuals use during the transient and settlement phases of dispersal (Travis *et al.* 2012; Elliot *et al.* 2014). Empirical studies that focused on the transient phase have concentrated on changes in movement characteristics and on the relationship between movement trajectories and the surrounding environmental landscape. The combined influence of the distribution and abundance of conspecifics – hereafter referred to as social landscape – on decision making during transience has received relatively little empirical attention, and related inferences are often based solely on theoretical work (Fletcher 2006;

93 Travis *et al.* 2012; Gilroy & Lockwood 2016). Yet the social landscape is likely to exert an
94 important influence on the behaviour of dispersing individuals during the transient phase.
95 In territorial social species such as the lion (*Panthera leo*), the African wild dog
96 (*Lycaon pictus*) and the meerkat (*Suricata suricatta*), encounters with unrelated groups and
97 individuals are often antagonistic and costly particularly for the smaller party (McComb,
98 Packer & Pusey 1994; Creel & Creel 2002; Mares *et al.* 2011). Dispersers are typically
99 outnumbered by resident groups, and thus, they may avoid areas where encounters with
100 resident groups are likely to occur. Such avoidance may be particularly strong in smaller
101 dispersing coalitions, and shortly before settlement, when dispersers seek an exclusive
102 territory. At the opposite end, the search for potential mates and high quality habitats during
103 transience and settlement may bring dispersers closer to resident groups (Andreassen & Ims
104 2001; Glorvigen *et al.* 2012). Whether dispersers are attracted to resident groups is likely to be
105 related to whether or not they can ever join them. Thus, dispersing male meerkats would be
106 expected to be attracted to resident groups, females to avoid them (Stephens *et al.* 2005; Mares
107 *et al.* 2011). In species that aggressively defend their territory from unrelated conspecifics and
108 where encounters can have fatal consequences, reducing costs of aggression may outweigh the
109 benefits derived from conspecific attraction (Stamps 2001; Fletcher 2006). Irrespective of
110 which strategy (conspecific avoidance or attraction) dispersers adopt during transience, their
111 ability to assess the social landscape at different spatial and temporal scales can reduce costs
112 and increase dispersal success (Bonte *et al.* 2012). Scent marks and other signs left by residents
113 convey information about their distribution and status (Jordan, Cherry & Manser 2007; Mares
114 *et al.* 2011; Jackson, McNutt & Apps 2012) and may be used by dispersing individuals to
115 indirectly gain information of the social landscape through which they move, avoiding risky
116 direct encounters.

A long-term study of the Kalahari meerkat (*Suricata suricatta*) (Clutton-Brock & Manser 2016) provides a unique opportunity to investigate the role of the social and environmental landscape during the transient phase of dispersal in a social and territorial species. Meerkats are territorial cooperative breeders living in groups of 5-40 individuals, and each group occupies an exclusive territory of 1-5 $km^2$ (Clutton-Brock *et al.* 1999; Jordan *et al.* 2007). Intruding meerkats, being dispersers or individuals from neighbouring groups, are readily challenged and chased by territorial groups, and such clashes can have severe consequences (Mares, Young & Clutton-Brock 2012). Groups are characterized by the presence of a dominant pair that monopolizes most of reproduction; subordinate individuals delay dispersal and help rearing their siblings. Older subordinate females are aggressively evicted from their natal group, and they form same-sex dispersing coalitions (Clutton-Brock *et al.* 1998). Encounters with the natal group after eviction typically result in aggressive behaviour directed towards the evicted individuals (Young *et al.* 2006). Dispersing coalitions either leave the natal territory and search for unrelated males and a place to settle, or they are sometimes let to re-join their natal group after the dominant female has given birth (Clutton-Brock *et al.* 1998). Subordinate females are, however, typically evicted in successive breeding attempts by the dominant female and eventually leave the area to form a new group (Clutton-Brock *et al.* 1998). Evictions happen year-round, but typically peaks between September and March (hereafter referred to as the dispersal season). Dispersing coalitions may have to travel a considerable distance to locate vacant territories and during this period experience costs of increased predation pressure and aggression from other meerkat groups (Clutton-Brock *et al.* 1999). In contrast to females, subordinate male meerkats spontaneously leave their natal group and prospect for extra-group mating opportunities. Such prospecting forays typically last few days, and a small proportion of them culminates in the males' dispersal or disappearance

141 (Young, Spong & Clutton-Brock 2007), likely after encountering a coalition of unrelated
142 dispersing females.
143 In this study, we aimed to investigate the effect of the social landscape on movement
144 behaviour and decision making during the transient phase of dispersal in a socially and
145 spatially structured species. To do so, we fitted GPS radio collars on dispersing coalitions of
146 Kalahari meerkats and followed their movements across territories occupied by constantly
147 monitored resident groups. We created environmental maps from satellite imagery to control
148 for the effect of habitat types, taken to represent different habitat quality, on movements. We
149 used step-selection models to quantify habitat and social selection of dispersers before and
150 after they left their natal territory. We regularly visited dispersers and collected information on
151 coalition composition to evaluate the effect of coalition size on selection of locations in the
152 social landscape during transience. Finally, we identified the temporal scale at which
153 dispersing coalitions perceived and reacted to the social landscape and investigated whether
154 they integrated information about the distribution of resident groups collected over different
155 weeks and months.
156
157 **METHODS**
158 **Study system and data collection**
159 The study site was located at the Kuruman River Reserve (S 26.92289°, E 21.84048) and the
160 adjacent ranch-land near Van Zylsrus, South Africa. The site includes a section of the fossil
161 Kuruman riverbed; elsewhere, the landscape is typical of the Kalahari Desert and is
162 characterized by sparsely vegetated sand dunes and dry pans (Fig. 1A). The climate is
163 characterized by a dry season between April and November and a wet season between
164 December and March, with 250 mm annual average precipitation. For further details on the
165 study site see Mares *et al.* (2012) and Young (2003).

166 The local population of wild meerkats has been subject of a long-term study started in
167 1993, and all study animals were individually marked. In any given year, between 15 and 18
168 resident groups that inhabit an area of 50-60 $km^2$ were regularly monitored. Resident meerkat
169 groups were habituated to the close presence (< 1 m) of researchers who visited the groups
170 every two to four days to collect behavioural and life-history data. During group visits, which
171 took place early mornings and late afternoons, and lasted three to four hours, researchers
172 consistently collected GPS locations every 15 minutes using a handheld GPS unit. We used
173 this spatial information on resident groups to create social landscapes (further detailed below).
174 We mounted GPS radio collars on subordinate dispersing females few days prior to or
175 immediately after eviction. We used behavioural cues such as aggression from the dominant
176 female, restless behaviour, and social withdrawal to identify potential disperser and anticipate
177 the time of eviction. We captured and anesthetized meerkats following a standardized protocol
178 used at the Kalahari Meerkat Project (Jordan *et al.* 2007). All captures were approved by the
179 South African Department of Environment and Nature Conservation and were performed under
180 permit 'FAUNA 192/2014'.
181 The GPS radio collars were composed of a 3.2 g stand-alone VHF beacon module
182 (Holohil Systems Ltd., Canada) and a 16.0 g stand-alone GPS module with integrated ZigBee
183 bidirectional communication capability powered by a 3.6 V ½ AA lithium battery (CDD Ltd.,
184 Greece). We casted the two modules in epoxy resins and used a 4.5 mm wide cable tie coated
185 with soft heat-shrink tubing to attach the unit to the neck of the animals. Overall collar weight
186 was < 25 g, corresponding to 3-4 % of the animal body weight. Collars of this size and weight
187 do not affect meerkats (Golabek, Jordan & Clutton-Brock 2008). Only one individual was
188 equipped with a GPS radio collar in each dispersing coalition at any given time. We
189 programmed the collars to collect hourly GPS locations between sunrise and sunset as
190 meerkats sleep underground at night. We additionally fitted few individuals with VHF-only

191 radio collars (Biotrack, United Kingdom) weighing approximately 23 g, when deploying GPS
192 collars was not possible for logistic reasons. For coalitions fitted with VHF-only collars, we
193 manually collected GPS information at each visit (Supplementary Material S1).
194
195 **Dispersing coalitions**
196 We defined a dispersing coalition as a single female or multiple females, evicted from the natal
197 group. We tracked each dispersing coalition by means of VHF telemetry every two to seven
198 days to record coalition size, which included females and, when present, unrelated males. We
199 defined a dispersal event as the collection of events starting at eviction and lasting until either
200 return to the natal group, settlement in a new territory, or death before settlement. We did not
201 include data collected after two weeks past successful settlement in a new territory as
202 coalitions may show resident-like behaviour after settlement.
203 Within each dispersal season (September – March), we merged consecutive dispersal
204 events by the same dispersing coalition in a single combined dispersal event (Supplementary
205 Material S1). For example, if two sisters were evicted from the resident group, then accepted
206 back into the group, and evicted again shortly after, these two events were considered as one
207 single dispersal event. This procedure reduced data dependence (two dispersal events of the
208 same coalition separated by a short period of time cannot be considered as independent) and
209 increased the data points of each combined dispersal event, which is a prerequisite for fitting
210 robust individual-level models for the step selection function (Craiu, Duchesne & Fortin 2008;
211 Fieberg *et al.* 2010; see below). During a three-year period, we monitored a total of 47
212 dispersing events, of which five were combined dispersal events consisting of two or three
213 consecutive events (Supplementary Material S1). Unless otherwise specified, all analyses were
214 performed using data from 47 dispersing coalitions.

We collected an average of 137 (range: 10 – 1114) GPS locations per dispersal event, which lasted on average 53 days (Supplementary Material S1). Twenty-seven coalitions re-joined their natal group after a variable duration of one (i.e. a coalition was evicted one day and allowed back to the group the following day) and 76 days. The remaining 20 coalitions did not return to their natal group and either dispersed for a minimum of six and a maximum of 284 days before settling in a new territory (n = 12 coalitions), dying (n = 3) or being lost (n = 5) before settlement.

**Creation of geo-referenced environmental layers**

Within R 3.2.0 (The R Foundation for Statistical Computing), we used the *rgdal* package to derive a geo-referenced digital elevation map (DEM) from Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) images (Fig. 1B). We further used NASA's Landsat 7 satellite images at 30x30 meters resolution to create a geo-referenced habitat map following an unsupervised classification approach using the function *kmeans* (Fig. 1A). Given the expected difference in reflectance between the vegetated sandy dunes and the dry 'pans', this unsupervised approach was adequate. Following ground-truthed data at 80 randomly selected locations, we merged the five classes (cfr. Fig. 1A) that resulted from the unsupervised classification into three main habitat classes; namely "pans", "sandy matrix", and "transition" between the former two classes. This procedure allowed us to achieve an accuracy of 98% for pans (1 in 45 pan locations was misclassified as transition), of 73% for sandy matrix (four in 15 matrix locations were misclassified as transition), and of 47% for transition. Pans were never misclassified as matrix and vice versa (for further details see Supplementary Material S2). The map obtained following this approach was very similar to vegetation maps for the study site used by (Bateman *et al.* 2015) and Google Earth imagery (Google Inc. 2012) thus confirming the reliability of the method (Fig. 1). Both ASTER and Landsat 7 images used are

240 available through the United States Geological Survey agency (http://www.usgs.gov).
241 Additionally, we used Google Earth to manually digitize and export the main channel of the
242 Kuruman River (Fig. 1).
243
244 **Creation of geo-referenced social layers**
245 We used GPS location data collected on resident groups to create a geo-referenced social
246 landscape (Fig. 1C). Because GPS locations on resident groups were collected every 15
247 minutes throughout a visit and were therefore highly spatially and temporally correlated, we
248 computed the harmonic mean of all locations collected during one visit resulting in one GPS
249 location per visit. For each resident group, we created a kernel utilization density (KUD) map
250 with the function *kernelUD* in the *adehabitatHR* package (Calenge 2006). We reduced the
251 reference smoothing parameter $h_{ref}$ until the smallest possible contiguous territory (i.e., one
252 single polygon) was obtained (Kie *et al.* 2010; Fieberg & Börger 2012). This procedure was
253 required because $h_{ref}$ typically over-smooths the data, inflating territory size. We used GPS
254 data collected during a time interval of 30 days prior to eviction of the dispersing coalition of
255 interest to create the KUD maps for each resident group. We excluded resident groups with
256 less than 10 locations collected over the 30-day interval to reduce the likelihood of unreliable
257 KUD estimation. We multiplied KUD pixel values by group size and summed KUD raster
258 maps of each resident group to create a contiguous social landscape comprising the distribution
259 and abundance of all resident groups for the given 30-day interval. Low pixel values
260 represented non-risky area characterized by a small likelihood of encountering resident groups,
261 while high pixel values represented risky areas. We assigned NA values to pixels with no
262 information on resident groups. For those dispersing events lasting more than two weeks, we
263 recalculated the social landscape with a two-week sliding window. This procedure allowed us
264 to create a dynamic social landscape. A social landscape was created using data on resident

groups collected within 30 days prior to eviction. The dispersing coalition of interest was then 'allowed to' move through this social landscape for two weeks (days 0 to 15 of the dispersal trajectory). If the dispersal event lasted more than two weeks, a second social landscape was created using data collected on resident individuals within 30 days prior to day 15 of the dispersal event. The same dispersing coalition was then 'allowed to' move through this new social landscape for two weeks (days 16 to 30 of the dispersal trajectory); and so forth (see Supplementary Material S3 for a dynamic representation of the social landscape).

To investigate at what temporal scales dispersing individuals perceive the social landscape, we repeated the same process for alternative time intervals of 45, 60, 75, 90, 105, 120, 150, 180, 240 days. In a final analysis, which we used as control treatment, we created a temporal mismatch between the social landscape and the dispersal events. For this, we created the social landscape by shifting back the beginning of each time interval by 180 days compared to the time of eviction of the dispersing coalition of interest. Because we assumed such a social landscape to be of little relevance for dispersers, we expected no consistency in their selection and avoidance of presumed risky areas.

**Statistical Analysis**

We used a step-selection function (SSF) to infer the effect of social and environmental covariates on habitat selection during dispersal (Fortin *et al.* 2005). Within this framework, the decision of a coalition to use a given location is conditioned on environmental and social characteristics at alternative locations (Fortin *et al.* 2009) that the coalition could have reached within an hour (the sampling interval between consecutive relocations). For each observed (i.e. used) step along a dispersing coalition path, we created ten alternative steps; the end of these steps represented alternative locations that the coalition could have chosen. A step is here defined as the vector between two consecutive relocations spaced one hour apart. We created

290 alternative steps by randomly drawing angles from a continuous uniform distribution U(0, $2\pi$)
291 and steps from a normal distribution N($\mu$,$\sigma$) with $\mu$ equal to two times the mean empirical step
292 length of monitored dispersing coalitions, with $\sigma$ equal to one step length standard deviation.
293 We chose $\mu$ to allow alternative relocations to be far from the relocation used by the focal
294 coalition, and thus to be characterized by different environmental and social factors. Dispersing
295 meerkats are bound to sleeping burrows, with new burrows being used as the dispersal process
296 progresses. While steps between consecutive burrows can be expected to be directional (i.e.
297 small turn angles), steps in the vicinity of sleeping holes are more circuitous (i.e. equally
298 distributed turn angles). As we could not distinguish between these two types, drawing angles
299 from a uniform distribution appeared more parsimonious.
300 Following this matched case-control design (Fortin *et al.* 2005), we built SSF using
301 conditional logistic regression to compare used (scored 1) and alternative (scored 0) locations.
302 The SSF took the general form
303 $$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_{n-2} x_{n-2} + \beta_{n-1} x_1 : x_2 + \beta_n x_1 : x_3)$$
304 where $\beta$'s are selection coefficients associated with covariates and biologically meaningful
305 interaction terms (Fortin & Fortin 2009). Steps with higher SSF scores w(X) are more likely to
306 be chosen by the animals (Fortin *et al.* 2005), and $\beta = 0$ indicates absence of
307 selection/avoidance (Forester, Im & Rathouz 2009). The environmental covariates considered
308 in the analyses included ELEVATION (continuous), DISTANCE TO RIVER (continuous),
309 and the binary habitat class PAN (coded 1 if a dispersing coalition was on a pan and 0 if
310 outside). We did not include the other two habitat classes (sandy matrix and transition) to avoid
311 collinearity with pans. The social variables were RISKINESS (the continuous social landscape
312 values), and NATAL (coded 1 if a dispersing coalition was within and 0 if outside the territory
313 boundary of the natal group). Because we anticipated that dispersing coalitions behave
314 differently within and outside the territory of the natal group, we included a RISKINESS by

315 NATAL interaction in our model. We also added dispersing COALITION SIZE as part of an
316 interaction term with RISKINESS to test whether coalitions of different size reacted differently
317 to the social landscape. Because each used and its ten alternative locations were assigned the
318 same coalition size, coalition size cannot appear in the model as a main effect (Fortin & Fortin
319 2009). We further defined a CLUSTER as the unique identifier for each independent dispersal
320 event, and a STRATUM as the unique identifier for each combination of used and alternative
321 locations. We used CLUSTER and STRATUM as grouping variables in the analyses (Fortin *et*
322 *al.* 2005). We implemented the above model in the *clogit* function in the *survival* package to
323 obtain population-level estimates of the selection coefficients associated with each covariate.
324 We calculated alternative SSF models with RISKINESS values obtained at each time intervals
325 (30, 45, …, 240 days) to detect the temporal scale at which dispersing coalitions showed the
326 strongest response to the social landscape (cfr. Fig. 3). We reported β coefficients associated
327 with all covariates only for the time interval that showed the strongest response.
328 In a second step, we used β coefficients obtained from conditional logistic regression
329 fitted to each coalition independently (Fieberg *et al.* 2010) to make inference on the effect of
330 additional coalition-specific covariates on step selection. We used linear regression to test the
331 effect of coalition size on estimated β coefficients, which were treated as response variables
332 (Thurfjell, Ciuti & Boyce 2014). Because some coalitions either never left the territory of their
333 natal group or almost only roamed outside of it (Supplementary Material S1), it was not
334 possible to fit a single model including the variable NATAL to each single dispersing
335 coalition. This was due to matrix singularities resulting from a coalition experiencing the same
336 events (e.g. all observed and alternative locations in a stratum have the same NATAL value).
337 We therefore ran two separate models; one with data collected when the dispersing coalitions
338 were within the territory of their natal group, and one when they were outside the natal
339 territory. To obtain robust coalition-specific estimations, we only retained dispersing coalitions

with a minimum of 30 used locations (see Craiu *et al.* 2008). Of the 47 monitored dispersing coalitions, 30 coalitions met this criterion while roaming within the territory of their natal group and 15 while outside (Supplementary Material S1). Like above, we run these two models only for the time window at which RISKINESS showed the strongest response.

In an additional analysis, we used a generalized additive mix model in the *mgcv* package (Wood 2004) to find the shape of any nonlinear relationship of RISKINESS over time (days since eviction) without imposing any specific parametric form. We averaged RISKINESS values on a daily basis to reduce autocorrelation issues. We allowed for differences between coalitions that returned to the natal group and coalitions that settled, while controlling for the effect of coalition size and the presence of unrelated males within a coalition. We included coalitions identity as random term.

## RESULTS

Movement patterns during dispersal were largely dependent on coalition size. Of the 47 dispersing coalitions monitored, the coalitions that settled (n = 12) were typically larger (mean = 2.3 females or 4.7 females and males) than the coalitions that returned (n = 33 coalitions; mean = 1.8 females or 1.9 females and males; Wilcoxon W = 116, p = 0.14 and W = 39.5, p < 0.01, for females or females and males respectively) (Supplementary Material S4). Average maximum displacement from the site of capture was 2'263 m (range 434 – 10'742 m). Coalition size showed a positive relationship with the log-transformed maximum distance travelled ($F_{1,46}$ = 6.14, p = 0.017) after correcting for differences in dispersal time.

After eviction from their natal group, dispersing coalitions selected for low-lying slacks between sand dunes and avoided pans (Table 1). Selection coefficients for PANS in four coalitions appeared implausibly large for an exponential model (e.g. -17.68; Table 2) and were likely due to matrix singularities. We therefore ran two alternative models: in one model, we

365 excluded these four coalitions, and in the other model we retained all coalitions but removed
366 PANS from the model. Results of coefficients of selection (i.e., ß values) remained unchanged.
367 Dispersing coalitions neither selected nor avoided locations closer to (respectively, further
368 away from) the fossil Kuruman riverbed. Dispersing coalitions reacted differently to the social
369 landscape depending on whether they were inside or outside the territory of the natal group
370 (RISKINESS:NATAL interaction term: $\beta = -0.055$, robust SE, 0.014, $p < 0.01$; Table 1). When
371 they were still within the territory of their natal group, they selected for locations characterized
372 by a higher likelihood to encounter the natal group. When they roamed outside the territory of
373 their natal group, they avoided locations characterized by a high likelihood of encountering
374 unrelated resident groups. These results thus support the hypothesis that dispersing coalitions
375 move in a way to minimize interactions with unrelated territorial groups.
376 Avoidance of risky locations outside the territory of the natal group persisted through
377 all time windows used to determine the social landscape, but the strength of risk avoidance
378 peaked at time windows between 60 and 75 days (Fig. 2). When we introduced a 180-day
379 mismatch between the social landscape and the time of eviction (see methods), we observed no
380 differences in the degree of selection of risky locations for areas inside and outside the territory
381 of the natal group (Fig. 2). This suggested that the social landscape is of relevance only within
382 a time intervals of a few months but is not informative over longer periods. Overall, adding
383 information about the social landscape to the baseline model that only accounted for
384 environmental variables improved model performance (log-likelihood ratio test for nested
385 models: $\chi^2 = 261$, $p < 0.01$, Supplementary Material S5).
386 Analysis at the coalition level did not support the hypothesis that smaller dispersing
387 coalitions avoided areas where encounters were likely to occur more than larger coalitions.
388 Although not statistically significant, there was an indication that selection for high-likelihood-
389 of-encounter areas decreased as dispersing coalition size increased (Fig. 3); both within (slope

390 = -0.013, SE = 0.009, p = 0.14) and outside (slope = -0.12, SE = 0.11, p = 0.31) the territory of
391 the natal group. Overall, results obtained at the coalition level (Table 2) largely supported the
392 results obtained at the population level (Table 1) showing that when dispersing coalitions were
393 within the territory of their natal group, they selected for areas characterized by a higher
394 likelihood to encounter the natal group (Table 2, Fig 3).
395 As time after eviction progressed, coalitions that settled increasingly used areas where
396 they were less likely to encounter conspecifics ($F = 17.2$, $p < 0.01$), whereas we could not
397 detect any relationship with time for coalitions that eventually re-joined their natal group. The
398 presence of unrelated males was associated with the use of areas characterized by a lower
399 likelihood to encounter resident conspecifics ($t = -3.4$, $p < 0.01$), both for coalitions that re-
400 joined their group and for coalitions that settled elsewhere, while coalition size had no
401 statistically significant effect ($t = -1.1$, $p = 0.3$).
402
403 **DISCUSSION**
404 Our study showed that, in a population of wild Kalahari meerkats, the movements of dispersing
405 individuals were influenced by the social landscape, i.e. the distribution and abundance of
406 resident conspecifics. Importantly, the reaction to this social landscape, depended on whether
407 dispersers were inside or outside the territory of their natal group. Before leaving their groups'
408 territory, dispersers appeared to maximise their chance of being in the same area as their natal
409 group. After leaving their natal territory, they selectively used areas where they were less likely
410 to encounter other unrelated groups, and increasingly so when unrelated males were part of the
411 dispersing coalition. This contrasting use of the social landscape suggests that dispersing
412 meerkats can acquire information on the distribution and abundance of conspecifics and use
413 this information to minimize antagonistic contacts with unrelated territorial groups.

414 Seeking proximity of the natal group despite the possibility of aggression, is consistent
415 with existing evidence of the advantages of group living and delayed dispersal in wild Kalahari
416 meerkats (Clutton-Brock *et al.* 1999; Clutton-Brock & Manser 2016). The tendency for
417 dispersing individuals to 'shadow' their natal group after being evicted was more pronounced
418 for smaller than for larger dispersing coalitions, suggesting that small coalitions may suffer
419 higher costs or gain smaller benefits by leaving their natal area. Associated costs may be direct
420 costs such as increased mortality due to reduced antipredator vigilance and dilution effect in
421 smaller groups (Delm 1990), or fitness costs associated with reduced recruitment rate in small,
422 newly formed groups (N. Maag pers. comm.).
423 Outside the territory of the natal group, moving through areas characterized by a small
424 likelihood of encountering unrelated resident conspecifics is likely to be beneficial since it
425 reduces antagonistic interactions and increase dispersal success. In the effort to avoid resident
426 groups, however, dispersers may move through suboptimal and resource-poor areas (Palomares
427 *et al.* 2000). While resident meerkat groups have been shown to concentrate along the edges of
428 the dry riverbed and surrounding flats habitats (Bateman *et al.* 2015), the dispersing coalitions
429 monitored during this study avoided such habitats (here referred to as pans). The riverbed and
430 pans offer more shelters (bolting holes) than the surroundings (Manser & Bell 2004);
431 avoidance of these safer habitats suggests that avoidance of resident groups may be a stronger
432 driver of habitat selection during dispersal than predation pressure. Such strategy may be
433 favoured by a relative low predation pressure; we only recorded one case of predation by a bird
434 of prey (on a single dispersers) and two meerkats were hit by cars. As food availability can
435 mask the effect of predation and conspecific aggression on habitat selection we urge further
436 investigation. In the Kalahari rainfall is highly variable both between and within years and it
437 affects food availability with consequences on meerkats growth and body condition (English,
438 Bateman & Clutton-Brock 2012). Changes in food availability may be partly responsible for

some of the variations in habitat selection observed among individual dispersing coalitions. This in light of the fact that the confidence intervals for the β coefficients of the habitat features considered were only lightly different from zero (which would represent no selection) and hence more susceptible to changes in selection or avoidance following alteration of the characteristics of the habitat itself.

Our results did not support the hypothesis that larger dispersing coalitions are competitively stronger than smaller coalitions and therefore less likely to avoid areas characterized by a high likelihood of encountering unrelated resident groups. This may be due to the fact that no matter how large a dispersing coalition may be, it will inevitably be substantially smaller than a resident group, which averages 15.5 individuals (Bateman *et al.* 2013), and therefore consistently avoid it. Our results suggest that rather than influencing movement patterns during transience, coalition size influenced the final outcome of the dispersal event – with smaller coalitions returning to the natal group and larger coalitions settling in new territories. Movements during transience were instead influenced by the presence of unrelated males and increasing time after eviction. Both factors caused dispersing coalitions to avoid areas with a high likelihood to encounter resident groups, suggesting that newly formed groups seek vacant or little used territories to settle. Mates thus not only influence dispersal patterns at emigration and settlement (Cote & Clobert 2007; Davidian *et al.* 2016; Gilroy & Lockwood 2016), but also during the transient phase. In fact, evidence suggests that, in meerkats, the association with unrelated males is one of the key drivers promoting the transition between the consecutive phases of dispersal (N. Maag et al. in review).

Results from our study also provide important insight into the temporal scale at which dispersing coalitions perceive and react to the social landscape. The underlying assumption of our analysis is that the GPS locations used to model the distribution of resident groups directly

464 correlate with cues of their presence and that dispersing coalitions perceive and react to such
465 cues. These may be direct encounters or indirect cues such as scent markings. Our analysis
466 showed strongest avoidance of areas characterized by a high likelihood to encounter unrelated
467 resident groups when the social landscape was modelled using GPS data collected on resident
468 groups during the 60/75-day interval preceding the dispersal trajectory. Using GPS locations
469 collected during shorter or longer time periods resulted in decreasing avoidance. We speculate
470 that a social landscape based on information collected during a too short period (< 30 days)
471 does not accurately represent the risks perceived by dispersing coalitions. The same applies to
472 social landscape based on information collected long before the dispersal event took place, as
473 suggested by our mismatch design (180-days timescale). These results suggest that care must
474 be taken in the temporal offset for the information used to create the social landscape.
475 The relative roles of direct and indirect cues in shaping dispersers' own representation
476 of the social landscape remains to be determined (Creel *et al.* 2005; Broekhuis *et al.* 2013). The
477 ability to predict risks related to distribution and abundance of conspecifics based on indirect,
478 long-lasting olfactory cues seems a parsimonious mechanistic explanation for a species that
479 relies on scent marking for between- and within-group signalling and communication (Jordan
480 *et al.* 2007; Mares *et al.* 2011; Bateman *et al.* 2015). While we have no direct evidence on how
481 long such cues may last for in meerkats under specific environmental conditions, reaction to
482 olfactory cues of several weeks to months has been documented for mammalian scent marks
483 (20-25 days: *Helogale parvula*; 65 days: sniffer dogs; 40-100 days: *Mesocricetus auratus*; 180
484 days: *Micricebus coquerely*) (Apps, Weldon & Kramer 2015). Our results suggest similar time
485 windows to be plausible for meerkats, but further investigation is required.
486 Our work, which focused on understanding the effects of the social landscape on
487 movement behaviour and decision making during the transient phase of dispersal, provides
488 empirical evidence for one of the "four areas where research effort should be directed", as

identified by Clobert et al. (2009) in their seminal review paper. Our results support the concept of socially informed dispersal (Clobert *et al.* 2009), where individuals gather social information during their movements. Empirical evidence if this applies also during the transience phase is critically lacking. The ability of dispersers to assess the topology of the social landscape influences how and where they move, with possible consequences on the settlement process. The latter can in turn influence the dynamic and persistence of structured populations. While we are only scratching the surface in understanding the proximate mechanisms and demographic consequences of dispersal, our results are an important step towards a better understanding of socially informed dispersal in a spatially structured species.

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**DATA ACCESSIBILITY STATEMENT** Data supporting the results of this manuscript is archived in the public repository Dryad (Cozzi *et al*. 2018; https://doi.org/10.5061/dryad.dk2pm).

**AUTHORS' CONTRIBUTION** GC, AO and NM conceived the study, NM collected data on dispersing groups, TCB led the collection of data on resident groups, GC and LB performed analysis, GC wrote the first version of the manuscript, and all authors contributed substantially to revisions.

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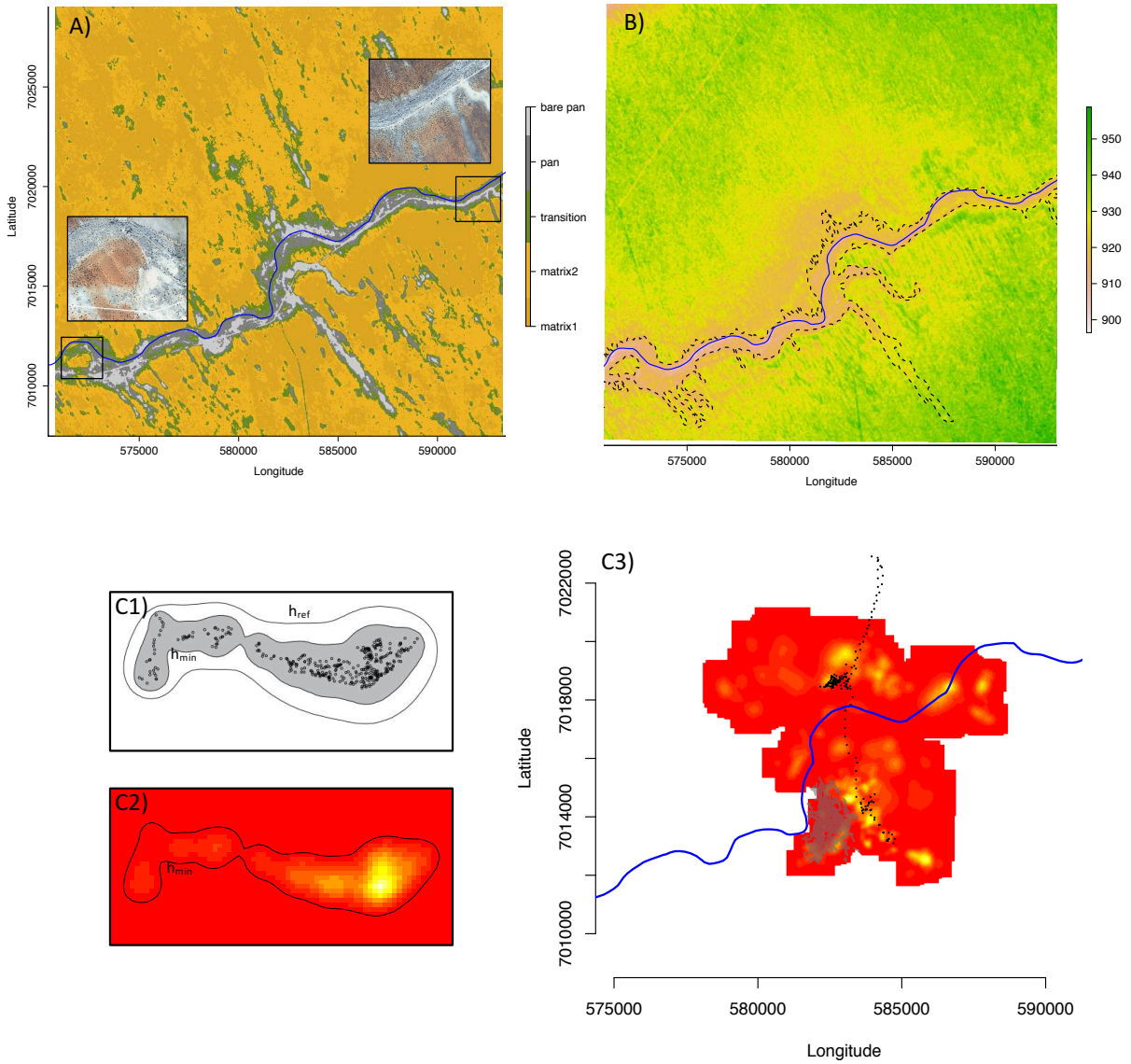
**Figure 1: Environmental and social geographic layers for the study area along the fossil Kuruman River, South Africa**. The site was divided in five discrete habitat types subsequently merged into three: pans, transition and sandy matrix (A). For comparison, Google Earth images have been inserted (framed inserts). A digital elevation model for the study area ranging between 890 and 960 meters above sea level was derived from ASTER imageries (B). A kernel utilization density (KUD) map for each resident group was calculated reducing the reference smoothing parameter $h_{ref}$ until the smallest possible contiguous territory (grey polygon) was obtained. Dots represent collected GPS locations (C1). KUD pixel values were then multiplied by group size. Light (yellow) colours represent frequently used regions (C2). KUD raster maps of each resident group were summed together to create a social landscape comprising all resident groups (C3). Example trajectories of a dispersing coalition that settled (dark dotted line) and a dispersing coalition that returned to the natal group (grey dashed line) are shown (C3). In all panels, the main river channel (solid blue line) are depicted for spatial reference.



703 **Figure 2: Dispersing coalitions step selection coefficients associated with the distribution**
704 **of resident groups.** The beta coefficients show the departure from baseline social landscape
705 values that dispersing coalitions select when moving within the territory of the natal group.
706 This means that when dispersing coalitions are outside the territory of the natal group they
707 select for areas characterized by a lower likelihood of encountering resident conspecifics.
708 Discrete social landscapes (real scenario) were calculated using GPS relocation data collected
709 on resident groups during alternative time intervals (30, 45, …, 240 days) prior to emigration
710 by the dispersing coalition of interest. For comparison, a temporal mismatch between the social
711 landscape and the dispersal events was created by shifting the time intervals used to create the
712 social landscape back in time by 180 days (mismatch scenario).
713

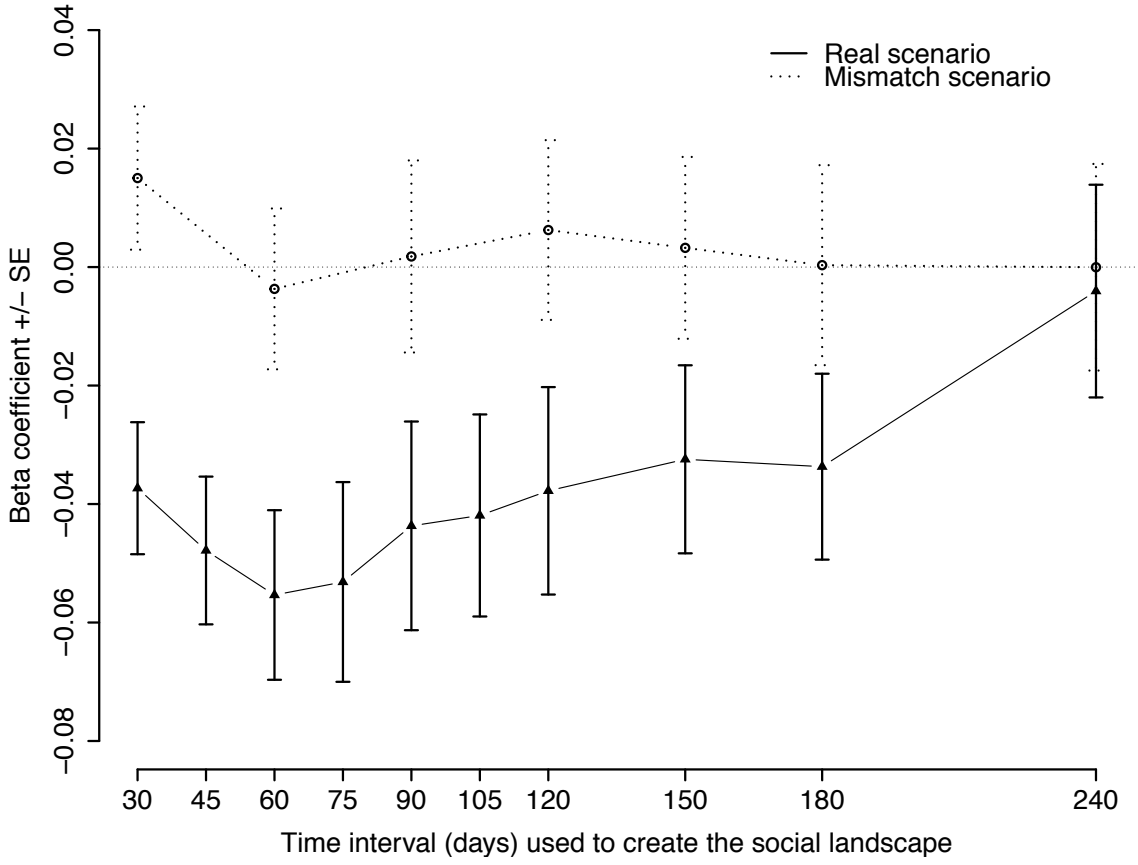



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**Figure 3: Coalition level relationship between selection for risky areas and dispersing coalition size**. Beta coefficients were obtained from SSF fitted to single coalitions and based on data collected while the coalitions where within (A) and outside (B) the territory of the natal group. Removal of the apparent outlier in (B) did not change the results. Note that Y-axes in (A) and (B) are on different scales.

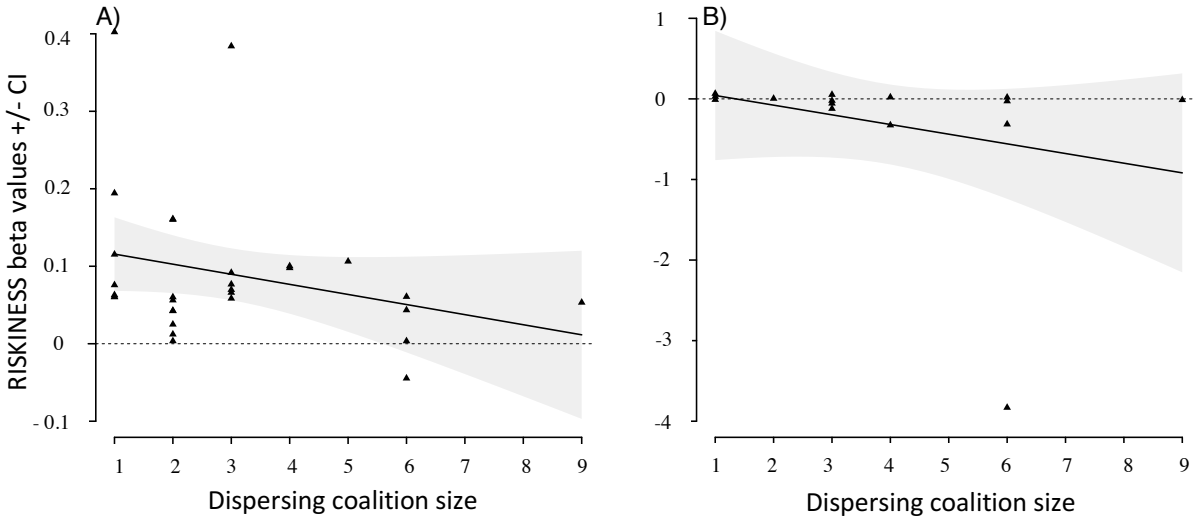

**Table 1: Population-level selection coefficients.** Coefficients and robust standard errors (S.E.) from a step selection function analysis where each observed location was conditioned on 10 alternative locations. Pans: factorial (whether a location is inside a pan or in the surroundings). Natal: factorial (whether a coalition is inside or outside the territory of the natal group). Riskiness: continuous values associated with the social landscape (range: $x \rightarrow 0$ to max(x)). Elevation and distance to river are measured in meters. Coal size: Maximum coalition size. Removal of distance to river did not change the results.

| | coefficient | S.E. | p-value |
|---|---|---|---|
| ELEVATION | -0.020 | 0.008 | 0.011 |
| PANS (inside) | -0.259 | 0.131 | 0.049 |
| DISTANCE TO RIVER | 0.000 | 0.000 | 0.440 |
| NATAL (outside) | -0.314 | 0.163 | 0.163 |
| RISKINESS | 0.059 | 0.009 | < 0.01 |
| NATAL(outside):RISKINESS | -0.055 | 0.014 | < 0.01 |
| COAL SIZE:RISKINESS | -0.005 | 0.003 | 0.090 |

759 **Table 2: Individual-level selection coefficients.** Coefficients and standard errors of
760 movement steps during dispersal regressed against environmental and social variables. For a
761 description of variables see Table 2.

762

| Inside NATAL | | | | | | Outside NATAL | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| COALITION ID | COAL SIZE | ELEVATION | PANS (inside) | DISTANCE TO RIVER | RISKINESS | COALITION ID | COAL SIZE | ELEVATION | PANS (inside) | DISTANCE TO RIVER | RISKINESS |
| | | β | | | | | | β | | | |
| 1 | 1 | -0.085 | -16.354 | -0.004 | 0.402 | 1 | 1 | -0.093 | -17.523 | 0.000 | 0.065 |
| 2 | 2 | -0.037 | -15.668 | 0.002 | 0.056 | 4 | 6 | -0.025 | 0.390 | 0.000 | -0.315 |
| 3 | 3 | 0.025 | -16.995 | -0.003 | 0.066 | 5 | 6 | -0.003 | -1.579 | 0.000 | -0.027 |
| 4 | 6 | -0.012 | 0.208 | -0.004 | 0.043 | 8 | 2 | -0.001 | 0.403 | 0.000 | 0.004 |
| 5 | 6 | 0.040 | -1.583 | 0.000 | 0.003 | 31 | 1 | -0.044 | 0.179 | 0.000 | 0.029 |
| 6 | 4 | 0.065 | -0.112 | 0.000 | 0.100 | 10 | 6 | -0.061 | -0.163 | 0.000 | 0.019 |
| 7 | 3 | 0.103 | -1.643 | 0.001 | 0.384 | 32 | 4 | -0.013 | -0.867 | 0.000 | 0.021 |
| 8 | 2 | -0.027 | 0.925 | 0.000 | 0.042 | 33 | 3 | -0.065 | 0.323 | 0.000 | -0.021 |
| 9 | 1 | 0.005 | -0.962 | 0.000 | 0.076 | 34 | 4 | -0.018 | 0.093 | 0.000 | -0.326 |
| 10 | 6 | -0.010 | -0.235 | 0.000 | 0.061 | 16 | 3 | 0.029 | -0.092 | 0.000 | 0.053 |
| 11 | 2 | -0.083 | -17.720 | 0.000 | 0.160 | 35 | 6 | -0.102 | -0.354 | 0.000 | -3.831 |
| 12 | 4 | -0.028 | -0.707 | 0.000 | 0.098 | 17 | 3 | 0.061 | -1.244 | 0.001 | -0.056 |
| 13 | 2 | -0.086 | -0.855 | 0.002 | 0.012 | 19 | 9 | 0.030 | 1.082 | -0.001 | -0.012 |
| 14 | 2 | -0.005 | -0.037 | 0.001 | 0.060 | 22 | 3 | -0.166 | -0.059 | 0.002 | -0.121 |
| 15 | 5 | -0.032 | 0.027 | 0.000 | 0.106 | 30 | 1 | -0.068 | -0.490 | 0.000 | -0.010 |
| 16 | 3 | -0.018 | 0.210 | 0.001 | 0.077 | | | | | | |
| 17 | 3 | -0.037 | -0.407 | -0.001 | 0.070 | | | | | | |
| 18 | 3 | -0.078 | -0.120 | 0.000 | 0.092 | | | | | | |
| 19 | 9 | 0.007 | 0.105 | 0.000 | 0.053 | | | | | | |
| 20 | 2 | -0.042 | 0.096 | 0.001 | 0.043 | | | | | | |
| 21 | 1 | -0.043 | -1.288 | 0.002 | 0.194 | | | | | | |
| 22 | 3 | -0.037 | -0.869 | 0.002 | 0.058 | | | | | | |
| 23 | 2 | -0.160 | 0.001 | 0.001 | 0.025 | | | | | | |
| 24 | 2 | 0.139 | -1.251 | 0.001 | 0.161 | | | | | | |
| 25 | 1 | 0.044 | 0.268 | -0.001 | 0.115 | | | | | | |
| 26 | 1 | -0.070 | -0.283 | 0.000 | 0.060 | | | | | | |
| 27 | 6 | 0.064 | -0.326 | 0.000 | -0.045 | | | | | | |
| 28 | 2 | -0.178 | 1.088 | -0.001 | 0.004 | | | | | | |
| 29 | 1 | 0.022 | 0.337 | 0.000 | 0.063 | | | | | | |
| 30 | 1 | 0.012 | 0.101 | -0.001 | 0.061 | | | | | | |

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